The Internal Anatomy, Reproductive Physiology, and Molting Process of *Ceratozetes cisalpinus* (Acarina: Oribatei)[1]

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ABSTRACT

All stages of *Ceratozetes cisalpinus* Berlese were sectioned successfully. Fixation in a modified Bouin's solution (with tetrahydrofuran substituted for the alcohol), with immediate puncturing, and embedding with a Tissuemat-N-butyl metacrylate provided excellent, undistorted sections of the heavily sclerotized adults; Tissuemat alone was sufficient for the immature stages. The molting process is divisible into a premolt and a hardening period, and one type of endocrine glands fluctuates in size, shape, and structure with the molting period. Except for the single pair of podosomatal glands, the smaller, more numerous dermal glands in immature stages are not the precursors of adult dermal glands; all dermal glands are associated with porose areas. The dorsal-opistosomatal gland (latero-abdominal of Grandjean) is poorly developed in this species. Salivary glands are formed from epidermal cells and are present only in adults. The epidermis disappears after adult sclerotization is complete. A central suspensory ligament forms a stable framework for muscle attachment in the region of the brain. The brain gives off 14 nerves, plus the ventral trunk. All tracheae originate from acetabula I and III, and each ends as a slightly swollen bulb. The digestive system comprises a stomodeum, a mesenteron, and a proctodeum; during molting a plug forms to block off each end of the mesenteron while the cuticular linings of the other two sections are replaced. The proventricular glands were found to contain green granules. Food flow is accomplished only by body-fluid hydraulic pressure and by further ingestion of food. The supracoxal gland is regarded as possibly being an excretory organ. The female matures up to 18 eggs at one time and deposits them simultaneously; the ovipositor is extruded by body-fluid pressure and retracted by special muscles. The penis is not an intromittent organ, but with the stalk-gland secretion forms the spermatophore.

Our knowledge of oribatid internal anatomy to date is based primarily on Michael's (1883) amazing hand dissections. The penis and the mouthparts of many oribatids have been described by Grandjean (1956b and 1957b). The internal anatomy of other groups of mites has been worked on more than that of oribatids, and Vitzthum (1943) offers a fine review of all work of this type down to 1940. Hughes and Hughes (1938), Hughes (1950), and especially Hughes' review (1959), Blauvelt (1945), Arthur (1960), and Gorirossi-Bourdeau (1956) have all contributed significantly to our understanding of the internal anatomy of mites other than oribatids.

The twofold purpose of this work is to present methods of sectioning armored oribatids and to present a general outline of the internal anatomy of a typical higher oribatid, *Ceratozetes cisalpinus* Berlese. No special attempt has been made to homologize or relate all oribatid internal structures to those of other mites or other Chelicerata.

METHODS

A culturing method (Woodring and Cook, in press) was necessary to obtain immature stages of known age, especially the quiescent premolt periods. It was found that only young adults, not more than 1 week old, would produce consistently good sections of all structures.

For both active and premolt immature stages, the best fixatives were standard aqueous Bouin's or tetra Bouin's (tetrahydrofuran is substituted for the alcohol of alcoholic Bouin's). After fixing the mites for

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12 hours in aqueous Bouin's they are placed in 70% isopropyl alcohol for 1 to 2 hours, then absolute isopropyl alcohol for 2 changes of ½ hour each, then 50:50 isopropyl-Tissuemat for 15 minutes, and finally in pure Tissuemat (54°-56° C. melting point). After fixing the specimens in tetra Bouin's for 2 to 3 hours, they are placed directly in absolute tetrahydrofuran for three changes of ½ hour each, then into 50:50 tetra-Tissuemat for 15 minutes, and finally pure Tissuemat (54°-56° C. melting point). The isopropyl-wax technique is modified from De Giusti and Ezman (1955), and the tetrahydrofuran (tetra) technique is from Salthouse (1958).

All solution changes were made with a fine-orificed dropper, and the specimens were never moved from the stender dish in which they were fixed. Puncturing in the fixative with an acid-sharpened needle was necessary to insure proper fixation for all stages of this species. The use of De Giusti and Ezman's modified Carnoy's solution and other strong fixatives gave poor results. Sublimates were no better as fixatives for Mallory's triple stain than was tetra Bouin's.

For young adults the same fixatives as for immature stages were found to be best. The Tissuemat-N-butyl metacrylate imbedding method of DeGiusti and Ezman (1955) was the only method which gave good adult sections. The standard double imbedding methods and various cuticle softening techniques were unsatisfactory. Specimens treated with the two above mentioned fixatives were treated as the immature stages up to absolute isopropyl alcohol or pure tetrahydrofuran, then placed in the monomer of N-butyl methacrylate (N-b.m.) and treated as DeGiusti and Ezman (1955) indicate (slightly modified) as follows:

1. Allow the monomer of N-b.m. to infiltrate the specimens for 3 to 4 hours at 54° C. (in stender dishes).

2. Place the specimens in a mixture of N-b.m., 2% to 3% accelerator (benzoyl peroxide) (vol. to wt.), and 2% Tissuemat (vol. to wt.) in an oven at 54° C. for 12 hours to polymerize. (This mixture is placed first in a small gelatin capsule, and polymerized enough so that the specimen does not go all the way to the bottom. The specimens are then placed in this partially polymerized mixture, and a bit more of the unpolymerized mixture is added.)

3. The gelatin capsule is removed by softening in water, and the plastic is trimmed to orient the specimen. (The plastic block should be twice as long and twice as wide as the specimen contained.)

4. Place the plastic block in molten Tissuemat (54°-56° C. melting point) for 10 minutes, then block, trim, and section.

Enough wax (about 2 mm.) must be left around the plastic block in order to get it to ribbon properly, and a device to combat static electricity must be employed. Routine sections were cut at 8 microns, but fair sections were cut as thin as 2 microns. Since the wax compresses slightly when sectioned, the plastic section will fold slightly. There is no displacement of structures in the comparatively uncompressible plastic. The sections must be stretched on the slide on a warming tray in order to remove the fold in the plastic section. The following is an excellent floating fluid and adhesive: 50 cc. of distilled water, 10 cc. of saturated sodium silicate, and 10 cc. of ammonium hydroxide. This is diluted 1:33 with water for use. The excess silicate adhesive must be removed after the sections are stretched. Xylol is a solvent for the plastic.

The monomer of N-b.m. can be obtained from most chemical houses, and the accelerator from Lucidol Division of Noadal-Agene Corp., 1740 Military Road, Buffalo 5, N. Y. The monomer of N-b.m. comes with a hydroquinone inhibitor, which must be removed. This is done by washing with 30% sodium hydroxide in a separatory funnel until the sodium hydroxide is no longer turned brown by the hydroquinone. With two washes with distilled water, and several passes through anhydrous $CaSO_4$, the N-b.m. is ready for use. It should be stored with some anhydrous $CaSO_4$ in it in a refrigerator. The mixture of N-b.m. monomer, wax, and accelerator can be kept in a refrigerator for several weeks. It is best to remove a small amount of the mixture 1 hour before use to prevent water condensation.

All stages were strained with Groat's (1949) haematoxylin or Mallory's triple stain. Sharp's modification of Mallory's triple stain for Protozoa (Kennedy 1932) proved to be the best triple stain for oribatid tissue.

INTEGUMENT AND CONNECTIVE TISSUE

Hughes (1959) states that endocuticle takes up basic dyes, and exocuticle acid dyes. He also states that white, flexible cuticle is sulfur-tanned, and that dark, rigid cuticle is quinone-tanned. Grandjean (1952) studied oribatid cuticle and found three layers, the exocuticle, endocuticle, and a waxy epicuticle. Quinone tanning is termed sclerotization, and tanning with either sulfur or quinones renders that cuticle unstainable with the stains used here.

Immature-stage body cuticle is sulfur-tanned externally and untanned internally. The thin, untanned inner layer stains with acid dyes. In order of intensity of sclerotization, the sclerotized areas for immature stages are: the gnathosoma, setal sockets, legs, porose areas, and the proterosomal plate. The untanned layer is lacking in the more heavily sclerotized regions.

Adult cuticle takes up acid dyes only in a thin inner layer in certain regions, and the thick outer layer does not stain at all. The venter of even the oldest adults still retain an acid-dye-staining, thin layer internally (fig. 28). Membranous areas, such as the notogastral membrane, take up acid dyes throughout the entire thickness. The cuticle of a 2-day-old adult does not stain at all; it is lightly sclerotized and the inner layers of exocuticle have not yet been secreted.

Sensory setae of any kind have a canal through

the cuticle (fig. 28). Respiratory and glandular porose areas (fig. 38) have many closely packed, minute canals penetrating the cuticle. A small, slightly sclerotized plate is formed on the outer surface of the sulfur-tanned cuticle of immatures where the muscles attach (fig. 29). In adults, areas of muscle attachment are thinner than surrounding areas.

The epicuticle is only visible in sections of adults, but is probably present in immatures also. This epicuticular wax layer (and possibly an oil on top of the wax) is probably responsible for the prevention of wetting of these animals in very high humidities. Debris clings to the cuticle for a while, but falls off or is rubbed off in a short time. Until the formation of a cerotegument in older adults, the cuticle of all stages is clean and glistening. The hard, dark concretion of fine particles of debris, or cerotegument, is discussed for this species by Woodring and Cook (in press).

The epidermis is retained throughout the immature stages, the cells becoming more numerous and active during the premolt period. The epidermis is retained in adults for 1 to 2 weeks during the completion of the formation and tanning of the cuticle. Except for an area on and around the anal and genital plates, the adult epidermis then completely disappears.

Other chitinous structures are: the linings of the pharynx and oesophagus, the genital atrium and discs, the ovipositor and penis, the trachea, and the rectal and colon linings. The cheliceral cavity (fig. 1) is lined with a thin, lightly sclerotized cuticle. The pharyngeal cuticle (fig. 40) is thick, pliable, and takes up acid dyes. The oesophageal cuticle is thick, grooved internally, and takes up basic stains. The junction of the pharynx and the oesophagus is just above the junction of the pedipalpal coxa-sternite with the venter of the body.

The cuticular lining of the rectum and the colon is best seen during the premolt period. It is very thin and takes up basic dyes. Near the anal opening the exocuticle becomes evident and forms an anal atrium (fig. 13).

The genital atrium is lined with endocuticle and the genital discs are also formed of it. The ovipositor is entirely exocuticle, and the surface that faces out when it is extruded is sclerotized. The vagina appears to be endocuticle.

The fecal pellet membrane first appears in the colon, and persists outside the body for several days (figs. 49, 50). The membrane stains with basic dyes.

The tracheae appear to be smooth and of a homogeneous structure, almost hyaline in appearance (figs. 46, 48). Tracheae appear only in adults, and may be seen as they are formed by epidermal-like cells in the tritonymphal premolt period (fig. 47).

A thin peritoneum covers every organ in the body, and the nuclei associated with this membrane can be easily seen. The basement membrane adheres to the cuticle in older adults when the epidermis degenerates. Many of the muscles, especially the longer and thinner ones, grade into tendons before reaching their point of attachment. Some of the fine, thin muscles supporting some organs are difficult to distinguish from various tendons and ligaments that connect the various organs one with another.

The central suspensory ligament (C.S.L.) is in the form of a short, transverse tube above the subesophageal ganglion (figs. 1, 9), and a diaphragm-like ligament divides this tube into a right and left half. The tube is supported at both ends by dorsal and ventral strands of connective tissue. The dorsal strands insert on the lateral region just below the notogastral suture, and the ventral strands insert on apodemata III. The C.S.L. stains blue in Mallory's triple stain, and red with periodic acid-Shiff reagent.

MOLTING

Oribatids become quiescent before molting, and will not move even if violently disturbed. This is called the premolt period. When the old cuticle splits, the new individual partly emerges and remains quiescent for a further definite period of time. This is called the hardening period. The molt is not complicated by extra skins, and is essentially like that described for *Scheloribates laevigatus* by Jones (1954). The molt from tritonymph to adult involves the appearance of many new structures. Salivary glands, mature sexual organs, tracheae, and various muscles are the most important. Except for the appearance of the fourth pair of legs at the larval molt, the molting of immature stages to another immature stage involves very little internal change. The old, untanned cuticle is dissolved away, and the sclerotized portion loosened. The pharyngeal-esophageal lining, genital atrium lining and genital discs, and part of the rectal lining are also loosened. Leg muscles detach and buds for new legs become active. The entire gnathosomal internal structure disintegrates, and buds for the various structures expand and form the new structures (fig. 51).

The new cuticle formed is always wrinkled before the old skin is split. The leg cuticle forms from the limb bud about halfway out of the old leg cuticle. When the new leg is formed, the leg is pulled up into the body cavity of the previous stage about midway in the premolt period. When the new cuticle is formed, and new muscles are attached, the old cuticle splits along what would be the notogastral suture from the posteriormost region of the hysterosoma up to the region of the fourth pair of legs. The new stage then expands to full size, and protrudes from the back. In the case of adults, it remains there for about 2 days while the cuticle hardens. If the specimen is released from the old cuticle before the hardening period is complete, the legs crumple and the specimen dies. The long setae of the immature stages are developed early in new cuticle formation, and then turn black about 12 hours before the old skin splits. A plug of unknown material blocks the anterior and posterior orifices of the mesenteron during the time a new fore- and hindgut are being formed (figs. 52,

53). Only the cecae and the mesenteron retain food in their lumens throughout the molt. Aside from the mesenteron, the most enduring structures are the brain and nerves, various glands, the central suspensory ligament, sex buds, and some muscles. Most of the cells of the hindgut are retained, and new cells are formed to enlarge the size of the hindgut. When the new lining is produced, the hindgut is again attached.

MUSCULAR SYSTEM

It is not within the scope of this work to identify every muscle in all stages of *C. cisalpinus*, but a few muscles are discussed here or elsewhere in this work. Since the adult is heavily armored, while the immature stages are soft bodied, the musculature of the opistosoma of adults and immature stages is quite different. The adult genital-plate-closing muscles originate on the preanal apodeme (fig. 1), and insert on the genital plates. Notogastral muscles appear to form groups that may indicate segmentation, there being major groups along the notogastral suture.

The adult anal-plate-closing muscles originate on the posterior portion of the notogaster. Many of leg III muscles originate on the C.S.L.; however, some of the leg III muscles and all the muscles for the other legs originate on apodemes, the median ventral ridge, or the lateral podosoma. Other adult muscles are drawn and labelled in figures 1 through 13.

Adults use the muscles to close the anal and genital plates, and fecal pellet or genitalic pressure to open these plates. Adults use the notogastral muscles to produce body fluid pressure to extrude the ovipositor, eggs, or penis, and rectal muscles to void fecal pellets. The immature stages use muscles to open the anal slit, and cuticular tension to close it. In immature stages the other opistosomal muscles are used mainly to void the fecal pellet.

The leg and gnathosomal muscles of the immature stages have reasonably rigid support on the proterosomal plate, apodemes or the c.s.l., and the musculature of this region is quite similar to that of the adults. The opistosomal muscles (fig. 30) of the immature stages are arranged to work together (or in opposition) so that not too much pull is put on one spot of the soft cuticle. The insertions of some of these opistosomal muscles often have very small sclerotized plates on the cuticular surface (fig. 29). Contraction of these muscles increases body pressure, and opens the anal slit. The fewer and weaker rectal muscles of the immature stages alone probably could not eject a fecal pellet as in adults.

The pharyngeal muscles (fig. 40) are arranged so the mite can suck up liquids, or take in solids by peristaltic movements. The pharynx is held in place by the ventral connective tissue block, which is attached by short, thick muscles to the pedipalpal coxasternum. Though esophageal circular muscles are large (fig. 56), longitudinal muscles are not discernible. Muscular valves between various sections of the gut are weak or completely lacking.

All muscles are probably striate, although in very thin muscles the striae could not be seen. The striations become more difficult to see in older adults. There are no muscles associated with the large setae of the immature stages and, therefore, the setae are incapable of independent movement.

BRAIN AND NERVOUS SYSTEM

Michael (1895) dissected out the brain of some oribatids, but did not indicate the nerves or the structure of the internal brain. In 1896 Michael did indicate the main nerves of a bdellid species, and Blauvelt (1945) traced the main nerves of *Tetranychus telarius*. The general shape of the brain and the origins of the main nerves are indicated in figure 27. The supra- and subesophageal ganglia are fused around the esophagus, there being both a medulla and cortex in the part lateral to the esophagus. The cheliceral and pedipalpal nerves are paired, as are each of the leg nerves. Accessory nerves, as shown by Michael (1896) in a bdellid species, could not be found. At the point where the supraesophageal ganglion abuts against the mesenteron an unpaired, thin nerve originates that proceeds towards the notogaster. The paired cheliceral nerves run to both the chelal and cheliceral muscles. The single median lingular nerve originates from the supraesophageal ganglion just above the point where the esophagus passes into the brain. The pair of pedipalpal nerves originates from the lower half of the commisures connecting the supra- and subesophageal ganglia. Each leg nerve branches almost immediately, innervating both the leg muscles in the body and in the leg proper. The unpaired, median, ventral trunk throws off a small digestive nerve first, then a large genital nerve. The genital nerve branches immediately to innervate the entire genital structure. A thin continuation of the ventral nerve extends to the region of the rectum, but could not be followed farther with the staining techniques used here. Undoubtedly the rectal muscles and the anal plate muscles are innervated by this last extension of the ventral nerve.

Sections of the brain are illustrated in figures 1, 7, 8, and 9. The medulla penetrates through the cortex where the main nerves originate. There is a distinct space between the neural lamella and the peritoneum of the esophagus, as the latter penetrates the brain. Only a thin layer of nerve cell bodies (cortex) is present on the dorsum of the subesophageal ganglion.

The main sensory organs of this species are the sensory setae of the legs, palps, venter of the body, and the pseudostigmatic organ. Neural canals penetrate the cuticle at the insertions of sensory setae (fig. 28) and of the pseudostigmatic organ (fig. 8). Pauly (1956) demonstrated that the first or second tarsi were sensitive to relative humidity. The notogaster of *C. cisalpinus* is devoid of setae, but the mite reacts even if touched very lightly there. Possibly, such pressure bends the legs, and muscular proprioceptors enable the mite to sense this pressure. The

various sensory setae, especially those of the tarsi, are probably chemoreceptors and/or contact receptors and the porose areas may be chemoreceptors instead of simply respiratory organs. Temperature receptive organs are unknown, according to Pauly (1956). He determined that the pseudostigmatic organs are sensitive to shock and shaking, and slightly sensitive to air movement.

DIGESTIVE SYSTEM

The mouthparts (figs. 1, 4, 5, and 6) are composed of two pairs of appendages, the chelicerae and the pedipalps. Berlese (1896b) sectioned the gnathosoma of *Oribatis globuli* and produced sections that appeared very similar to *C. cisalpinus* sections. Grandjean (1957a) compared the internal capitulum and chelicerae of many oribatids. Hughes' (1959) postulation that acarine mouthparts are derived from only two segments is found to be the most acceptable. The first segment is the cheliceral, and the second the pedipalpal with its appendage the palps. The lingula is considered here as an elongation of the dorsal wall of the pharynx, even though it is separately innervated.

The works of Berlese (1896a) on *Neoliodes theleproctus* and Hughes (1950) on *Tyroglyphus farinae* were very useful in the investigations of *C. cisalpinus*' digestive tract. The digestive tract of *C. cisalpinus*, schematically drawn in figure 39, is identical but for size in all stages. The foregut and hindgut are lined with chitin and supplied with muscles, while the midgut has no apparent muscles and certainly no chitinous lining. Only circular muscles are evident around the oesophagus, while both circular and longitudinal muscles are evident encasing the hindgut. The circular muscles are innermost. The colon muscle layers are much thinner than the rectal muscle layers.

Berlese (1896a) divided the hindgut of *N. theleproctus* into the intestine, colon, and rectum, while Hughes (1950) divided the hindgut of *T. farinae* into colon and postcolon. *C. cisalpinus* has two sections, the colon, which is slightly convoluted, and the heavily muscled rectum. A short anal atrium (fig. 13) is present between the genital plates and the beginning of the rectal cells.

The chitinous interior surface of the esophagus is ridged as in figure 41. The inherent structure and opposable muscles of the pharynx (fig. 40) make it a very efficient sucking tube. Peristaltic muscle action permits solid food to be taken up easily.

The cells of the mesenteron are large, have a striate border, and contain many granules (figs. 42 and 54). The nuclei are large, round, and conspicuous. The digestive caeca open on the posterior lateral region on both sides of the midgut, and extend back to the end of the body cavity. These caeca are squeezed towards the notogaster, and their volume is decreased when the sex organs of both sexes are fully developed and functioning. In gravid females, the caeca may be squeezed flat. The cells of the caeca are similar to those in the mesenteron, except that vacuoles are present (fig. 43). Apparently, certain caecal cells become highly vacuolated, enlarge tremendously, lose their striated border and nuclei, and finally burst and disgorge the vacuole contents into the lumen. Dark, shriveled, highly granulated cell remains are interspersed among the other cells.

The proventricular glands appear to be simply a few enlarged cells of the mesenteron (figs. 42 and 54). The nuclei are lacking, and they are packed with greenish, hyaline granules. These green granules are shaped like mammalian red blood cells. The other mesenteron cells have scattered granules of the same size and shape, but they are not colored green. The proventricular gland (Michael 1883) is present in all stages.

The function of the green granules is unknown. By means of indicator dyes, Hughes (1950) concluded that the stomach (mesenteron) and caeca of *T. farinae* secrete carbohydrate and protein digestive enzymes, and absorb the products. Very likely, the same would apply to *C. cisalpinus*.

The cells of the colon (fig. 45) are much smaller than those of the mesenteron. They are generally tall and slender, but vary in tallness. When sectioned longitudinally, the cells appear to be grouped as in figure 1. Dispersed among the colon cells are larger, highly vacuolated cells. The lumen border of the colon cells seems to be more of a brush border than just a striate one.

Hughes (1950) states that the colon regulates the pH of the food bolus, and is the site of the formation of a peritrophic membrane in *T. farinae*. The colon of *C. cisalpinus* forms and solidifies the food bolus, and possibly, although this is not proven, some absorption takes place. The membrane around the food bolus first appears distinctly in the colon. This membrane takes up basic dyes, and envelopes the food bolus completely (figs. 49, 50). Mucus is probably secreted in the mesenteron, as it is in *T. farinae*. We assume that it is this mucus (or mucoid substance) that forms the membrane around the food bolus and fecal pellet in *C. cisalpinus*, and that a chitinous peritrophic membrane is not formed. Grandjean (1948) believes the fecal pellet membrane in oribatids is probably lucifuge (a mucoid).

The rectum, or colon (Berlese 1896a), and post colon (Hughes 1950), is illustrated in figure 39. Here in *T. farinae*, according to Hughes (1950), water is absorbed and the food bolus is compacted. Probably also in *C. cisalpinus* water is absorbed here, and certainly the food bolus is given its final compaction and shaping. The cells (fig. 44) are tall and thin in the ventral portion, becoming shorter and broader in the dorsal portion. The nuclei are small and dark. Vacuoles are prominent, as is a striate border. The striate border and vacuoles are less evident in the dorsal portion than in the ventral portion. In the ventral portion long, compact masses of rods (brush border) support the food bolus. Sometimes strands of membrane work loose at the dorsal

surface of the food bolus and float in the lumen of the dorsal portion of the rectum. The chief function of the rectum seems to be storage and voiding of waste products.

The flow of food through the digestive system of the immature stages can be observed directly through the semitransparent cuticle. The flow of food to and from the caeca was not determined because there did not seem to be any regular flow or flow pattern. Since there are no muscles associated with the stomach and caeca, the flow of food between the caeca and stomach must be regulated by body fluid pressure and incoming food pressure. The caeca of the immatures are relatively larger than those of the adult.

The entire digestive tract is supported at only two points. Anteriorly it is supported at the junction of the esophagus and the stomach by the central suspensory ligament, and posteriorly by a few muscles that run from the rectum to the posterior portion of the notogaster.

RESPIRATORY SYSTEM

Much work has been done on the oribatid respiratory system, as viewed externally, by Grandjean (1934, etc.) in many papers. There are two types of respiratory systems in oribatids. These are the primary type which is formed of the acetabula and tracheae, and the secondary type which is formed of the porose areas found mostly on the legs. Grandjean (1933b) found tracheae in immature of *Eremaeus* spp. and *Hermanniella* spp., but apparently the vast majority of immature oribatids, including *C. cisalpinus*, lack tracheae. In immature *C. cisalpinus*, respiratory porose areas occur only on the legs and proterosomal plate. Very likely cutaneous respiration takes place through the soft cuticle of the body. Respiratory porose areas occur on all the legs of the adult. The respiratory porose areas of adults occur only on the trochanters and femora, while in the immatures these areas occur on the coxae, trochanters, and femora.

Adult tracheae originate only from acetabulae I and III as illustrated in figure 31. The entire tracheal system was not traced out, but some general observations for this species can be made. The tracheae are smooth, simple tubes that always end in a bulb (fig. 1). Branching of the tracheae takes place only close to the acetabulae or from one of the three main tracheal trunks. The number of tracheae is small, but the average length of the tracheae exceeds the total body length. The tracheae wind and twist through the whole body, but never enter the legs.

EXCRETORY SYSTEM

Neither malpighian tubules nor any of the other excretory organs described for other groups of mites were found in *C. cisalpinus*. The supracoxal gland (figs. 3, 57), as described by Michael (1883), has an uncollapsible lumen produced by a spiral thickening throughout its length (figs. 31, 32). The spiral thickening and the lumen wall appeared to be cuticular. The lumen ends blindly posteriorly as the gland loops anteriorly. The external orifice of the lumen of the supracoxal gland is minute, but can clearly be seen on the posterior surface of acetabulum I. Like all other internal organs, the supracoxal gland has a peritoneal covering. The nuclei of the cells are small and show little structure. Striations can be seen in the cytoplasm, proceeding from the lumen to the peritoneum. The lumen content is a homogeneous material that cannot be identified. This gland (or organ) is present also in all immature stages, and empties to the exterior just above leg I. The supracoxal gland might be an excretory organ, though the possibility of its being a gland of some other type cannot be excluded.

REPRODUCTIVE SYSTEM

Michael's (1883) work remains the best to date on the oribatid reproductive system. The reproductive system can be traced only by sectioning young adults since in older adults the various parts expand and become very difficult to trace.

The female system is illustrated in figures 11, 12, 14 through 21, and 59 through 62. The single median ovary is surrounded by a double membrane, the interior one being the ovarial tunica propria and the exterior one the peritoneum. The ova develop on a central ovarial stalk or medulla (figs. 20, 62), which is not attached to the tunica. The more mature ova are always close to the ovarial bulb, and when completely developed break the connection to the ovarial stalk and enter the oviduct via the ovarial bulb. At maturity, the ova are about 0.045 mm. in diameter. Fertilization occurs in the oviducts, and a blastoderm is formed before the egg is deposited. Development appears to be panoistic. The eggs are kept in the oviducts until they are all at the same stage of development, and then are deposited all at one time. The oviduct at this time is tremendously enlarged and elongated, taking up virtually all the space in the female body. On the average 12 eggs are matured and fertilized at one time, though up to 18 have been observed in one female.

The ovarial bulb is an enlarged portion of the oviduct that attaches to either side of the ovary. No muscles have been observed associated with it, though a membrane appears to line the lumen. This bulb may act as a one-way valve, but the exact mechanism of moving the mature ova into the smaller oviduct is unknown.

Though a muscular and cuticular lining may be present in the oviduct, they could not be demonstrated. The follicular epithelium of the oviduct becomes more vacuolated as the egg matures. When the eggs are deposited most of the follicular cells disintegrate. The oviducts from both sides join the median vagina just over the dorsal surface of the ovipositor.

The vagina seems to be mostly a cuticular tube with many small flat cells between the cuticle and peritoneum (fig. 21). Eggs pass through the vagina,

but are never held here. The vagina forms the inside surface of the proximal portion of the ovipositor when it is extruded.

The ovipositor is a chitinous, muscular, telescoping tube that can be retracted by means of muscles that have their origin on the notogaster (fig. 14). These muscles lie between the vagina and the proximal ovipositor when the ovipositor is extruded. When the ovipositor is retracted the insertion of the ovipositor-retracting muscles can be seen to insert at the junction of the distal and proximal ovipositor. The ovipositor wall is composed of thin muscle bands with the cuticle folding in between each band (fig. 21). Longitudinal muscles are present in the distal portion of the ovipositor, especially in the fingers of the ovipositor.

Extrusion of the ovipositor is probably accomplished by egg pressure and body fluid pressure. The genital discs probably keep the genital atrium open by means of powerful muscles that originate on the wall of the podosomal region and insert on the closed end of the genital discs during the increase of body fluid pressure (fig. 10).

The developing ovipositor is pictured (fig. 59) about three-fourths of the way through the tritonymphal premolt period. The female genital bud just beginning to expand during the early tritonymphal premolt period is pictured in figure 61.

The ovipositors of *C. cisalpinus* (fig. 17) and other oribatids are discussed by Woodring and Cook (in press).

The female picks up the sperm ball in the genital atrium, then by some unknown means ruptures the sperm sac. Whether the sperm are forced by pressure up the ovipositor or proceed under their own power into the oviduct is unknown.

The paired testes rest partially upon a separate posterior lobe of the seminal vesicle (fig. 22). The germinal layer rests upon the peritoneum tunica. Sperm formation is of the packet type; that is, where a group of germinal cells undergo meiosis together and remain in a group. The meiotic products remain together in the testes, through the seminal vesicle, vasa deferentia, and finally into the spermatophore (fig. 23). A membrane to hold the sperm together could not be demonstrated. The germ cells and chromosomes are very small; the metaphase plate appears as a dark line under oil immersion. It could not be determined whether spermatids or spermatozoa are present in the spermatophore. Sperm tails were never seen (fig. 23). Pauly's (1956) illustration of the sperm of *Belba gracilipes* shows no tail and shows that the sperm is of the same size and shape as found here for *C. cisalpinus*.

The seminal vesicle cells are vacuolated, and contain dark irregular concretions (figs. 24 and 25). The nuclei of these cells are large and stellate. Muscles could not be demonstrated in the walls of the seminal vesicle. In mature adult males, the seminal vesicles enlarge greatly (fig. 13), and can store up to a dozen sperm packets. The seminal vesicle sphincter is composed of a thick band of muscle (fig. 24). The function of this sphincter may be to control the passage of sperm packets into the vasa deferentia.

The vasa deferentia are attached at one end to the seminal vesicle sphincter, and at the other end to the top of the penis.

The penis is a spermatophoric organ, not an intromittent one. The action of a male of this species depositing a spermatophore is described by Woodring and Cook (in press). Grandjean (1956b) described the penial sclerites and associated setae of *Damaeus onustus*. The penis of *C. cisalpinus* has either five or six penial sclerites, each with what appears to be a seta at the tip. These sclerites are short and very well supplied with muscles. There is also a sclerite (control sclerite) that acts as a valve between the opening of the vasa deferentia and the stalk gland (fig. 26). There are many muscles of the penis that are not connected to any of the sclerites. Some of these muscles act as sphincter muscles and close the entrances of the stalk gland and the vasa deferentia simultaneously. When these sphincter muscles dilate, the control sclerite then is able to close either the opening to the stalk gland or the vasa deferentia separately.

The stalk gland is a hollow ball of small cells of irregular height. The lumen of this gland is lined with cuticle. A thin band of muscles is present between the glandular cells and the exterior layer of epithelial cells. These muscles probably expel the stalk-forming material when the penis is extruded.

On the dorsal, anterior, median surface of the genital atrium appears a group of highly vacuolated, glandular-appearing cells. These cells are continuous with the epithelial cells covering the stalk gland and also with the ventral epidermis. This gland (atrial gland) is not present in females. It is postulated here that the products of this gland form the membrane of the sperm sac (fig. 23).

The stalk material formed by the stalk gland is apparently stuck to the substrate and drawn out into a stalk by the penial sclerites. The stalk material seems to harden on contact with air. The exact mechanism of placing a sperm packet in a fluid surrounded by a membrane to form a sperm sac and then suspending this sac on the stalk is unknown.

The various parts of both male and female organs are connected to other parts of the respective organs by means of fine ligaments or muscles (figs. 10 to 13). The female system is supported anteriorly by the genital discs, and posteriorly by the ovipositor retracting muscles. The male system is supported anteriorly by the genital discs, but posteriorly there seems to be no support.

The number of genital discs varies regularly according to the stage, but the structure is essentially the same for all stages (fig. 10). Larvae have no discs, protonymphs have one pair, deutonymphs two pairs, tritonymphs and adults three pairs. A genital disc is a chitinous, tubular, transverse structure open laterally and closed mesally. Large muscles insert

on the closed end of the tube from origins on the lateral body surface.

The primary function of the genital discs is probably to maintain the stability of the genital atrium while the ovipositor or penis is being extruded. Extrusion of the genitalic structure is accomplished by body fluid pressure developed by the contraction of notogastral muscles. The discs never protrude from the body of a living mite, although dead females show the discs externally. Dead adults often have the entire genitalia and parts of the rectum everted through the genital and anal plates, respectively, due possibly to the pressure of gases and liquids resulting from decay.

Developing male and female genitalia can be differentiated after the first day of the tritonymphal premolt period (figs. 61, 64). Even the gonads may be distinguished at this time, as shown by the female gonad in figure 61. During the second day of the tritonymphal premolt period, the ovipositor is clearly formed in outline. The indifferent genital system of a tritonymph is sketched in figure 15. The sex tubes are formed and connect the gonad to the genitalic bud. The sex may be determined during the later tritonymphal stage by whether or not the gonad is bilobed posteriorly; if bilobed, it is a male. There is a narrow, flattened genital atrium in all nymphal stages, but it does not open to the exterior. Deutonymphs lack the sex tubes, and the genitalic buds are smaller. Protonymphal and larval genital buds are composed of just a few cells which are difficult to distinguish from the surrounding epidermis.

GLANDS

The glands of oribatids, exclusive of digestive glands and gonads, have been studied by Grandjean (1929, 1933b, 1939, 1950) and Michael (1883), but only the latter has dissected oribatids and no one has ever sectioned them.

All adult, and most immature, body porose areas are gland openings. There are two types of glands that open through porose areas. The first are typical dermal glands (figs. 29, 38, 48). Six pairs of large dermal glands occur on the lateral surfaces of the notogaster of adults (fig. 10). Immature dermal glands are much smaller and more numerous (fig. 29). Immature dermal glands are not precursors of adult dermal glands. All dermal glands are derived from epidermal cells (fig. 38). The cells of an adult dermal gland are highly variable, and it is suspected that not all are functional at any one time. Some dermal gland cells are highly vacuolated, almost to the point of being hollow, while others are much smaller, with sometimes no vacuoles at all. Immature stages seem to possess two types of typical dermal glands, one type associated with the setal sockets of the dorsal opistosomal setae and the other type associated with a very small, lightly sclerotized, porose area. There is no atrium or lumen for any of the typical dermal glands; the cellular products if any must proceed directly through the small pores of the porose areas associated with these glands. The exact function of the products of these typical dermal glands can only be guessed at.

The second type of gland that opens to the exterior via a porose area is the single pair of podosomal glands (figs. 10, 11, 36, 58). This gland is present in the adult and all immature stages in much the same form. In immature stages a special sclerotized, oval, porose plate is present dorsal to and slightly anterior of leg III. Grandjean (1929, 1939) described the external opening of this gland in *Ceratozetes gracilis* and in a number of other higher oribatids. The gland forms a hemisphere of very symmetrical, tall thin cells over the porose area leading to the exterior. The nuclei are all at the same height in the cells, and though vacuoles are lacking, many small granules that become more numerous in the nucleus-containing end of the cell are present. The function of the podosomal gland can only be speculated on at this time.

Another gland that is common among higher oribatids, but is poorly developed in this species, is the paired dorsal opistosomal gland (figs. 12, 13). Grandjean (1950) discusses the structure and functioning of this gland which he called the latero-abdominal gland. In *C. cisalpinus* this single pair of glands forms a long, flattened sack, and is composed of very small cells. There is a homogeneous material in the lumen of this gland, but the exterior opening is very minute. The external opening is in the form of an inconspicuous slit, and the connection to the gland is so tenuous that probably no functional connection is present. In other species, this gland has larger cells, the lumen is larger, and the connection to the large external opening is distinct and clear.

Salivary glands are present only in adults (figs. 1, 7, 55, 34), and are derived from epidermal cells (fig. 51) during the tritonymphal premolt period. The salivary gland consists of about eight lobes, each with its own lumen. The lumen of each lobe empties into a large common salivary duct, which immediately splits into a right and left branch. The salivary ducts empty on either side and slightly anterior to the middle of the lingula (figs. 1, 56). The salivary cells form a single layer in each salivary lobe, and are highly vacuolated, with large distinct nuclei (fig. 34). The vacuoles appear to empty their contents in the lumen of each lobe. The probable function of the saliva produced would be lubrication and to some degree digestion. Why the immatures lack these glands when their diet and that of the adults is very similar is unknown.

There are two sets of glands that lack both a lumen and an opening to the exterior. These are the three pairs of coxendocral glands (figs. 10, 31, 35, 57), and the single pair of lateral glands (figs. 10, 37, 58). The lateral gland on each side is composed of about six to eight large cells lying just ventral to the podosomal gland. It is always attached to the lateral body wall in all stages of this species. During molting the cells of this gland are much

larger, are more vacuolated, and stain much less intensively (fig. 58) than before or after molting. In the adult stage the cells are more darkly staining and shriveled-appearing than during any other stage. (fig. 37). Since the lateral gland becomes very active during molting, it is reasonable to assume the products of this gland are connected with the molting process. Just what this connection is cannot be said at this time.

Each coxendocral gland appears as a ball of four to six cells lying in the region of acetabula III. Two of these glands are located on and closely appressed to each of the supracoxal organs, one dorsal and one ventral to the ventral arm of the supracoxal organ. Only the ventral one is illustrated in figure 31. A single gland is present on each side, just mesal and ventral to acetabulum III. These glands appear unchanged in all stages of this species. The cells of the coxendocral glands are tightly appressed to one another, and no peritoneum was seen to surround these glands. Each cell has a large vacuole toward the center of the gland, and a very small nucleus toward the outside. Granules are uniformly distributed throughout the cells. The function of these glands is unknown.

PARENCHYMA

The body spaces are packed with parenchyma cells. These are almost completely dissolved away with ordinary fixatives, leaving only scattered nuclei and cell membranes (figs. 11, 33). Probably food reserves are stored here, but in what form is unknown. Hughes (1950) found the parenchyma of *Tyroglyphus farinae* to contain glycogen, while Blauvelt (1945) determined that fat made up that of *Tetranychus telarius*.

Occasional groups of small, loose cells were seen lying near the epidermis or near some organ (fig. 33). For lack of a better name, these were called blood cells. Though the parenchyma seems completely to fill the body cavities of this species, considerable quantities of fluid are released when a living specimen is crushed.

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FIG. 1 SAGITTAL SECTION S_1

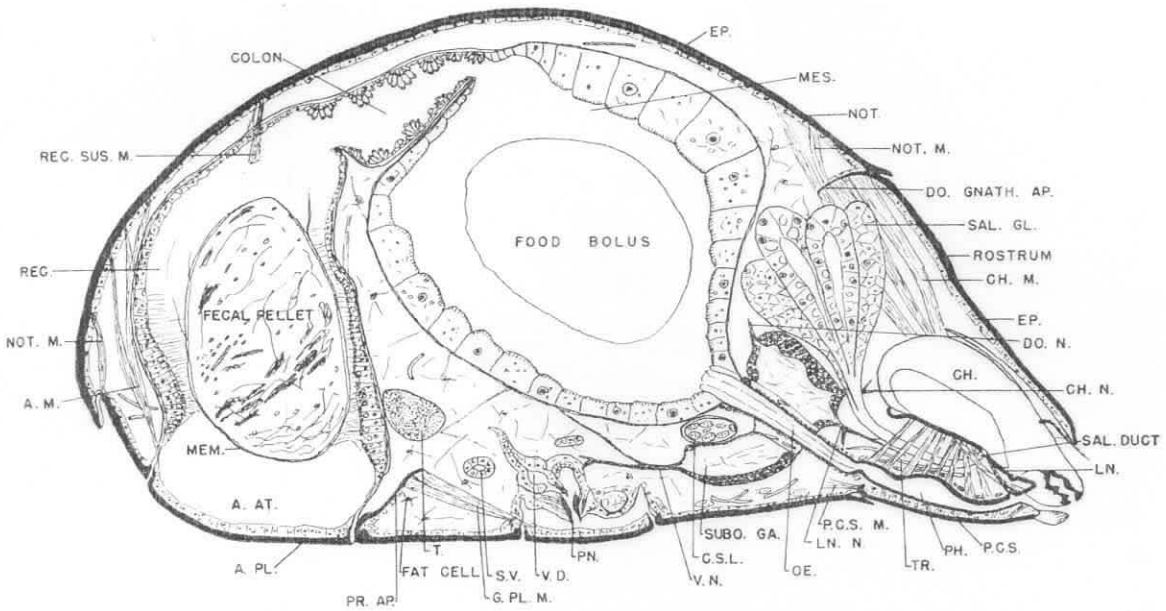

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FIG. 2 KEY TO SECTIONS

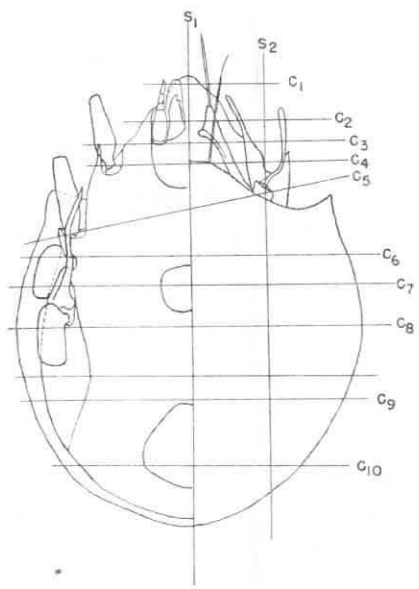


FIG. 3 SAGITTAL SECTION S_2

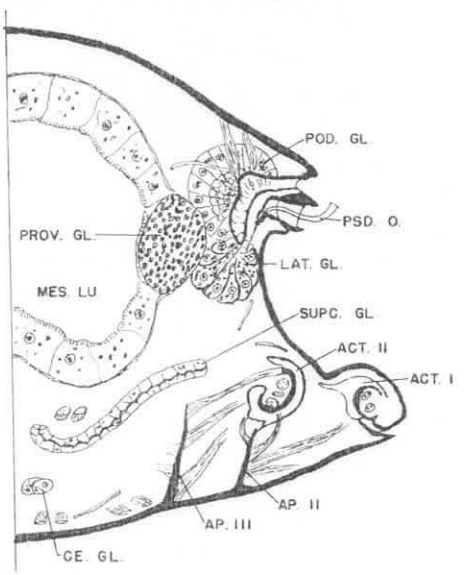


FIG. 4 CROSS SECTION C_1

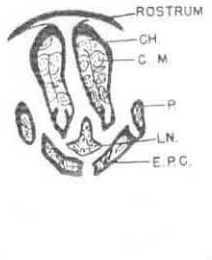


FIG. 5 CROSS SECTION C_2

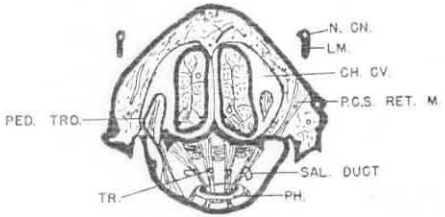
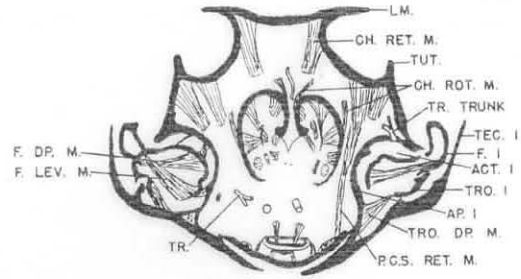


FIG. 6 CROSS SECTION C_3



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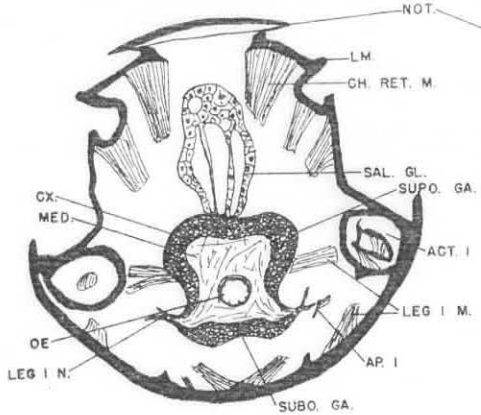


FIG. 8 CROSS SECTION C_5

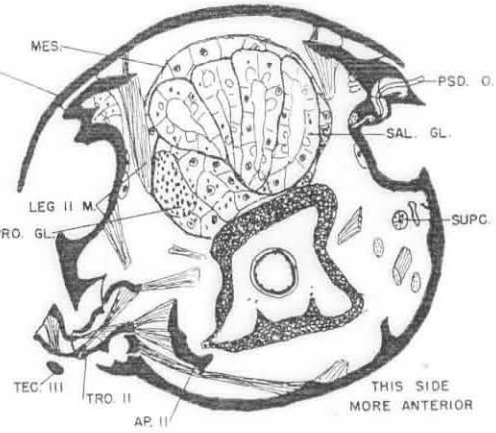
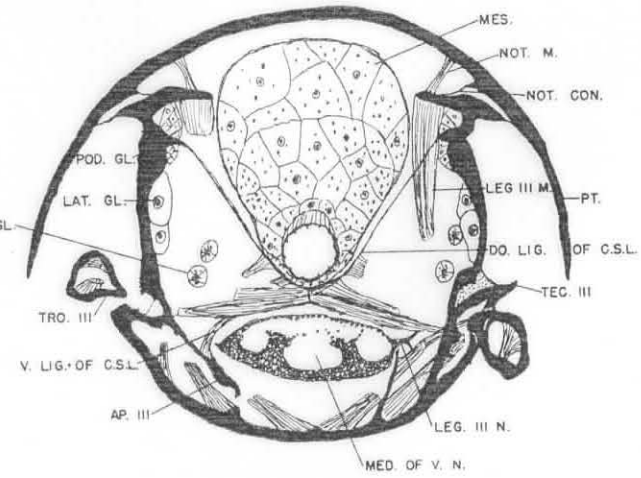


FIG. 9 CROSS SECTION C_6



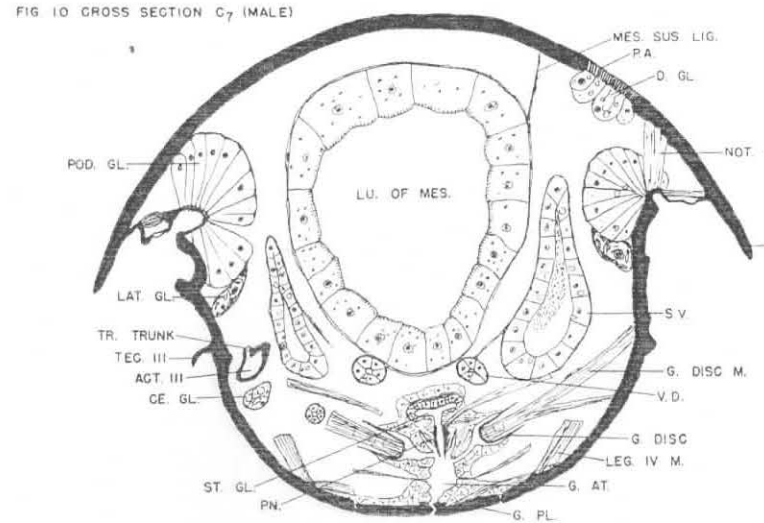


FIG. 10 CROSS SECTION C_7 (MALE)
MES. SUS. LIG.
P.A.
D. GL.
NOT. M.
POD. GL.
LU. OF MES.
PT.
LAT. GL.
S.V.
TR. TRUNK
TEG. III
ACT. III
CE. GL.
G. DISC M.
V.D.
G. DISC
LEG. IV M.
ST. GL.
G. AT.
PN.
G. PL.

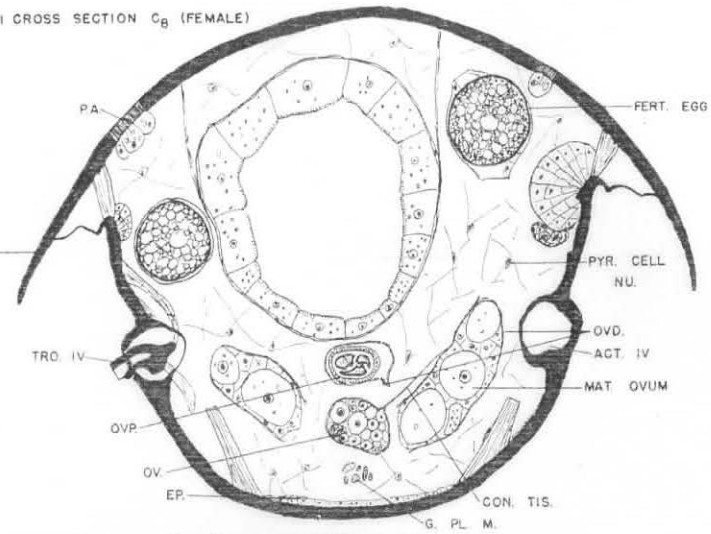


FIG. 11 CROSS SECTION C_8 (FEMALE)
P.A.
FERT. EGG
PYR. CELL NU.
OVD.
TRO. IV
ACT. IV
MAT. OVUM
OVP.
OV.
EP.
CON. TIS.
G. PL. M.

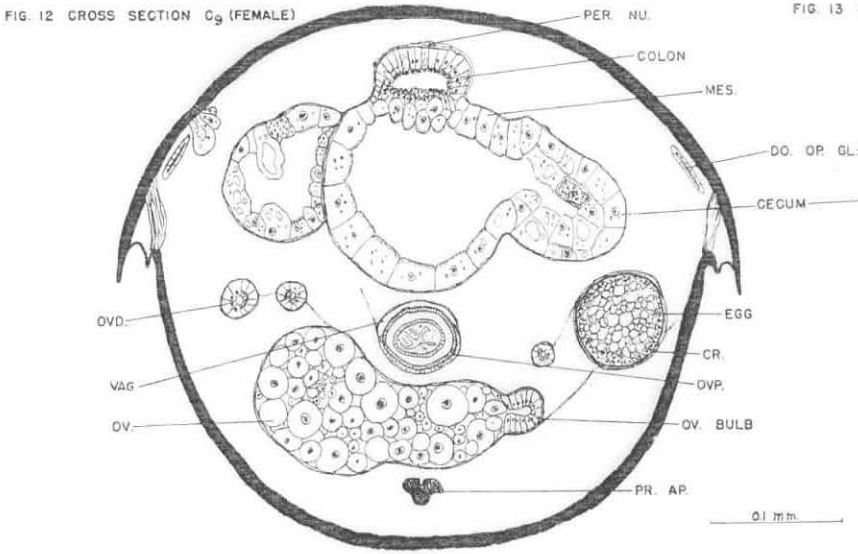


FIG. 12 CROSS SECTION C_9 (FEMALE)
PER. NU.
COLON
MES.
DO. OP. GL.
CECUM
OVD.
EGG
CR.
VAG
OVP.
OV.
OV. BULB
PR. AP.
0.1 mm.

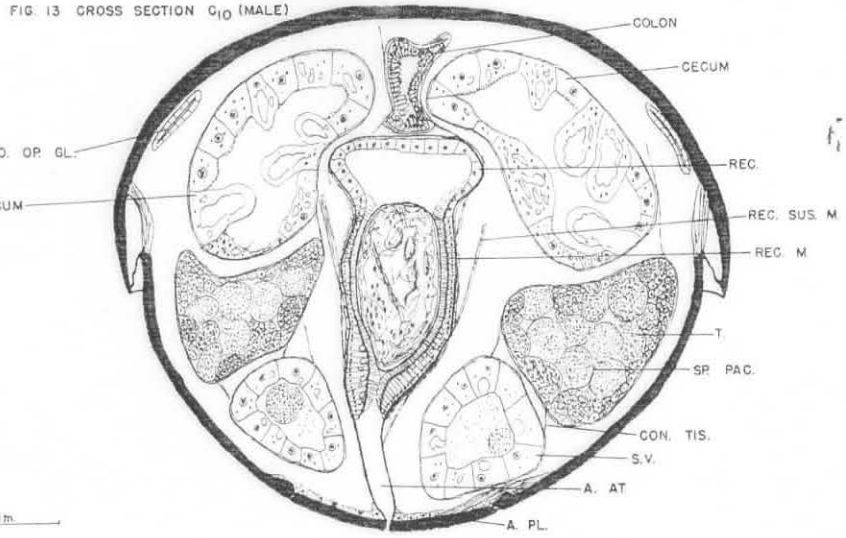


FIG. 13 CROSS SECTION C_{10} (MALE)
COLON
CECUM
REC.
REC. SUS. M.
REC. M.
T.
SP. PAC.
CON. TIS.
S.V.
A. AT.
A. PL.

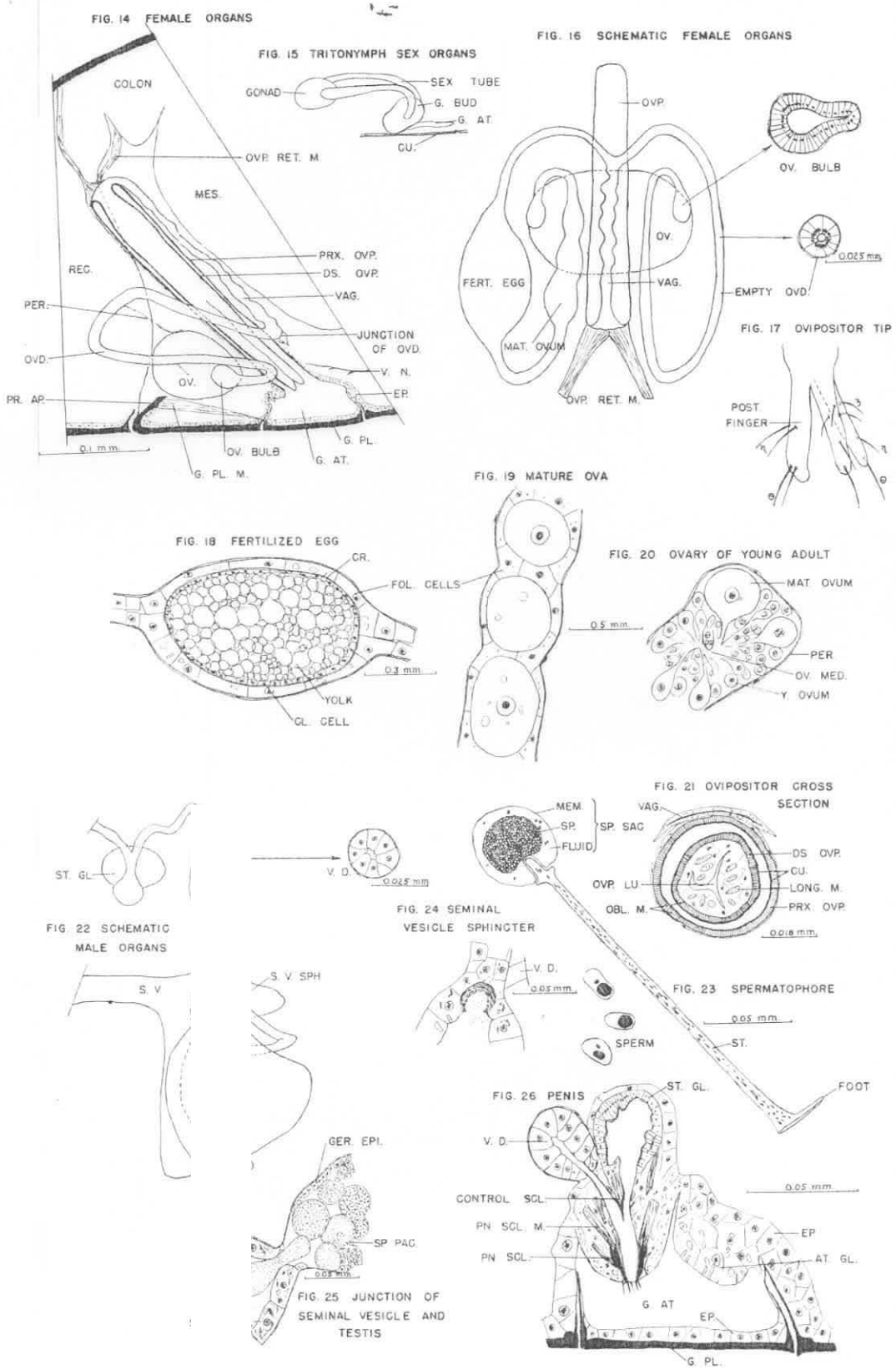
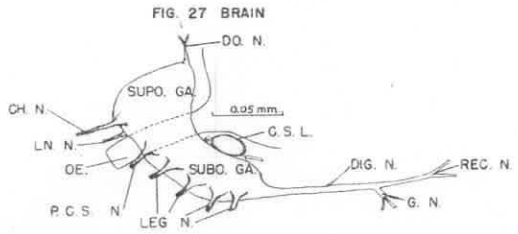
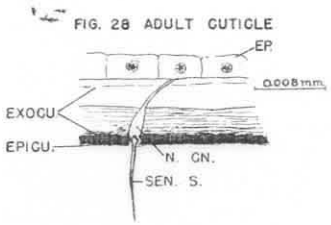
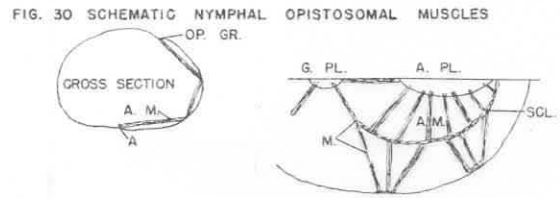
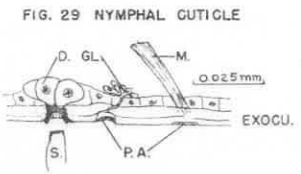


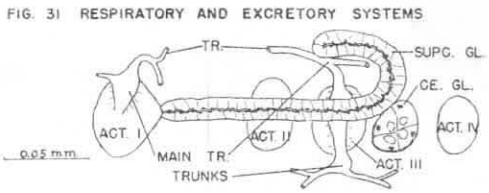
FIG. 14 FEMALE ORGANS
COLON
OVP. RET. M.
MES.
REC.
PRX. OVP.
DS. OVP.
VAG.
PER.
JUNCTION OF OVD.
OVD.
V. N.
OV.
EP.
PR. AP.
G. PL.
0.1 mm.
OV. BULB
G. AT.
G. PL. M.
FIG. 15 TRITONYMPH SEX ORGANS
GONAD
SEX TUBE
G. BUD
G. AT.
CU.
FIG. 16 SCHEMATIC FEMALE ORGANS
OVP.
OV. BULB
OV.
0.025 mm.
FERT. EGG
VAG.
EMPTY OVD.
MAT. OVUM
OVP. RET. M.
FIG. 17 OVIPOSITOR TIP
POST. FINGER
FIG. 19 MATURE OVA
0.5 mm.
FIG. 18 FERTILIZED EGG
CR.
FOL. CELLS
0.3 mm.
YOLK
GL. CELL
FIG. 20 OVARY OF YOUNG ADULT
MAT. OVUM
PER.
OV. MED.
Y. OVUM
FIG. 21 OVIPOSITOR CROSS SECTION
MEM.
SP.
FLUID
SP. SAC
VAG.
DS. OVP.
CU.
OVP. LU.
LONG. M.
OBL. M.
PRX. OVP.
0.018 mm.
ST. GL.
FIG. 22 SCHEMATIC MALE ORGANS
V. D.
0.025 mm.
FIG. 24 SEMINAL VESICLE SPHINCTER
S. V.
S. V. SPH
V. D.
0.05 mm.
FIG. 23 SPERMATOPHORE
0.05 mm.
SPERM
ST.
FOOT
FIG. 26 PENIS
ST. GL.
V. D.
0.05 mm.
CONTROL SCL.
PN SCL. M.
EP.
PN SCL.
AT. GL.
G. AT.
EP.
G. PL.
GER. EPI.
SP. PAC.
0.05 mm.
FIG. 25 JUNCTION OF SEMINAL VESICLE AND TESTIS

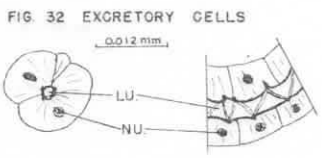


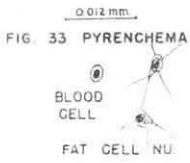


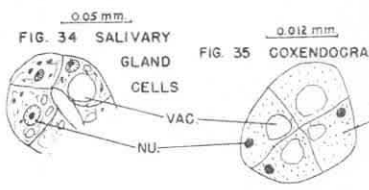


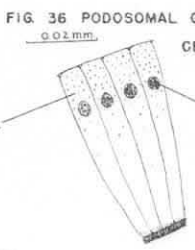


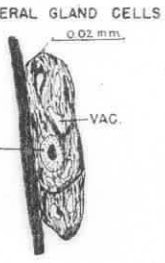


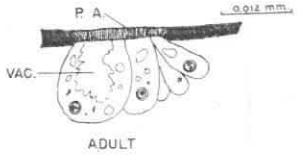












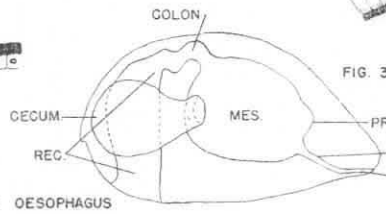
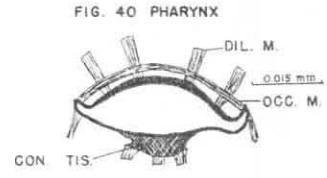


FIG. 39 SCHEMATIC DIGESTIVE SYSTEM



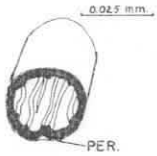
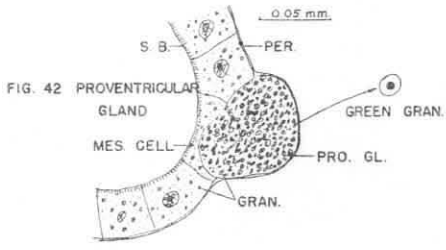
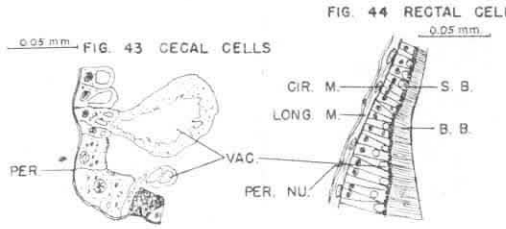
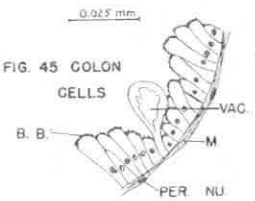


FIG. 41 OESOPHAGUS







ABBREVIATIONS IN FIGURES 1 TO 45

A.	Anus; anal	CR.	Chorion
ACT.	Acetabulum; acetabula	C.S.L.	Central suspensory ligament
AP.	Apodeme	CU.	Cuticle
AT.	Atrium	CV.	Cavity
BB.	Brush border	CX.	Cortex
C.	Chela	D.	Dermal
CE.	Coxendral	DIG.	Digestive
CH.	Chelicera	DIL.	Dilator
CIR.	Circular	DO.	Dorsal
CL.	Cleavage	DP.	Depressor
CN.	Canal	DS.	Distal
CON.	Connective	EP.	Epidermis; epidermal

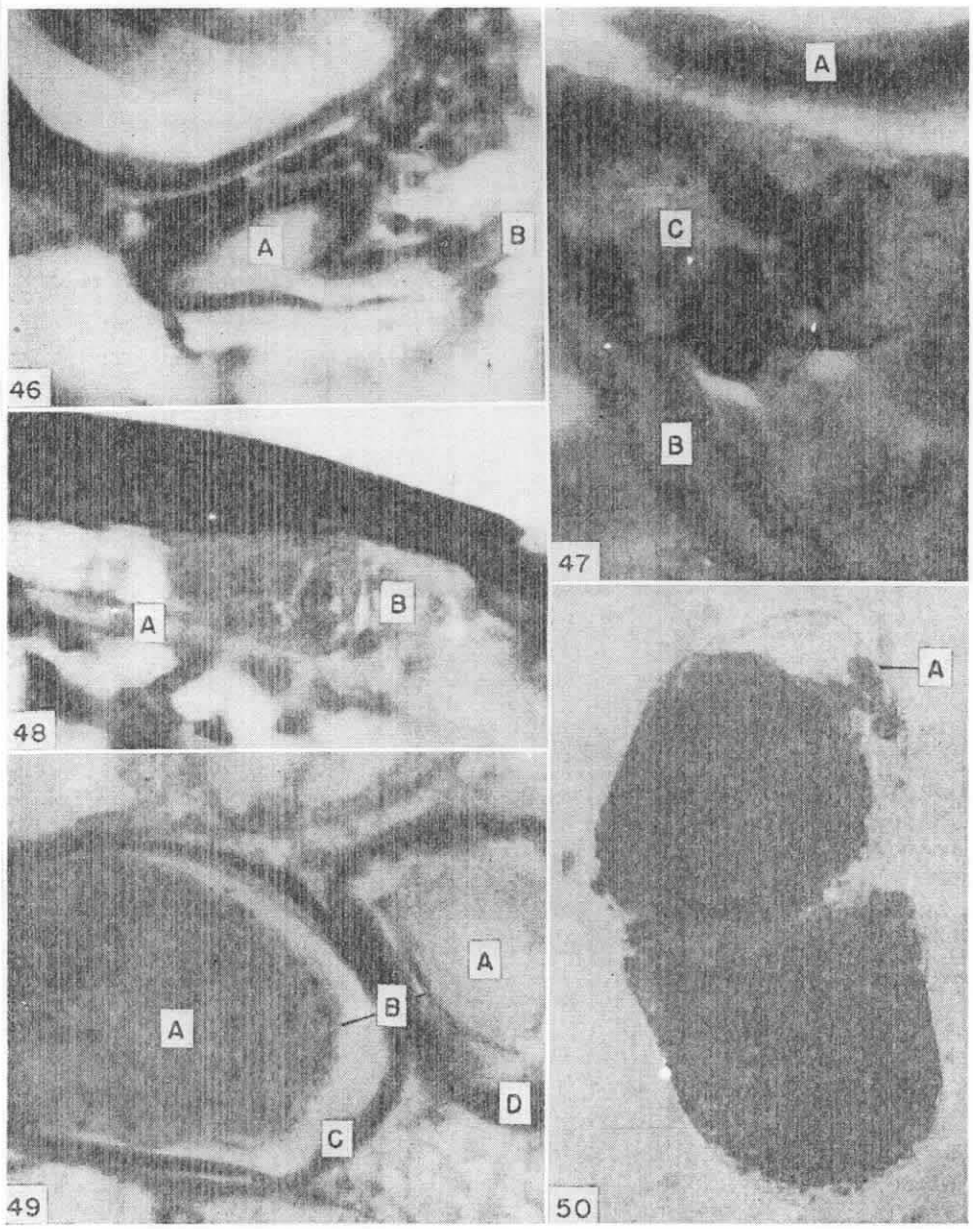


FIG. 46.—Adult: A, acetabulum I; B, trachea. FIG. 47.—Premolt tritonymph: A, developing pteromorph; B, developing trachea; C, lateral gland. FIG. 48.—Adult: A, trachea; B, typical dermal gland. FIG. 49.—Adult: A, food bolus; B, membrane; C, rectum; D, colon. FIG. 50.—Fecal pellet: A, membrane.

E.P.C.	Endite of pedipalpal coxa	LM.	Lamella
EPI.	Epithelium	LN.	Lingula
F.	Femur	LONG.	Longitudinal
FERT.	Fertilized	LU.	Lumen
FOL.	Follicular	M.	Muscle(s)
G.	Genital	MAT.	Mature
GER.	Germinal	MED.	Medulla
GL.	Gland	MEM.	Membrane
GN.	Gnathosoma	MES.	Mesenteron
GR.	Groove	N.	Nerve
GRAN.	Granules	NOT.	Notogaster; notogastral
LAT.	Lateral	NU.	Nucleus
LEV.	Levator	O.	Organ
LIG.	Ligament	OBL.	Oblique

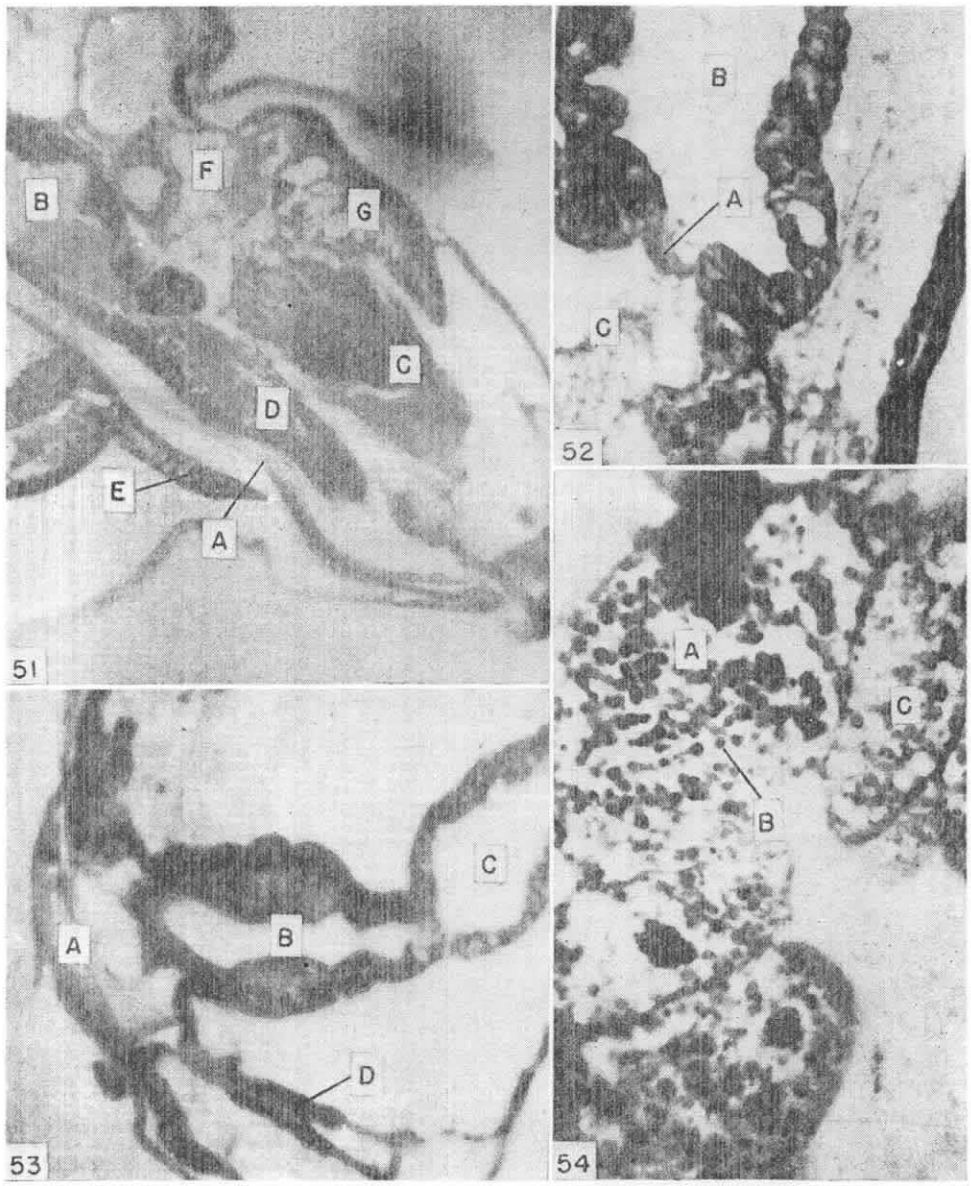


FIG. 51.—Developing adult gnathosoma: A, junction of pharyngeal and esophageal cuticle; B, supra-esophageal ganglion; C, cheliceral bud; D, lingular bud; E, pedipalp coxae-sternum bud; F, developing salivary gland; G, rostral bud. FIG. 52.—Premolt tritonymph: A, colon plug; B, colon; C, mesenteron. FIG. 53.—Premolt tritonymph: A, anal plate; B, developing rectum; C, developing colon; D, anal-plate closing muscle. FIG. 54.—Adult: A, proventricular gland; B, green granule; C, mesenteron cell.

OCC.	Occlusor	ROT.	Rotating
OE.	Esophagus	S.	Seta
OP.	Opistosome; opistosomatal	SAL.	Salivary
OV.	Ovarial; ovary	S.B.	Striated border
OVD.	Oviduct	SCL.	Sclerite; sclerotized
OVP.	Ovipositor	SEN.	Sensory
P.	Palp	SP.	Sperm
P.A.	Porose area	SPH.	Sphincter
PAC.	Packet	ST.	Stalk
P.C.S.	Pedipalpal coxa-sternum	SUBO.-G.	Subesophageal ganglion
PED.	Pedipalp; pedipalpal	SUPC.	Supracoxal
PER.	Peritoneum	SUPO.-G.	Supraesophageal ganglion
PH.	Pharynx	SUS.	Suspensory
PL.	Plate	S.V.	Seminal vesicle
PN.	Penis; penial	T.	Testis; testes; testicular
POD.	Podosomatal	TEC.	Tectopodia
POST.	Posterior	TIS.	Tissue
PR.	Preanal	TR.	Trachea; tracheal
PRO.	Proventricular	TRO.	Trochanter
PRX.	Proximal	TUT.	Tutorium
PSD.	Pseudostigmatic	V.	Ventral
PT.	Pteromorph	VAC.	Vacuole
PYR.	Parenchyma	VAG.	Vagina
REC.	Rectum; rectal	V.D.	Vas deferens
RET.	Retractor	Y.	Young

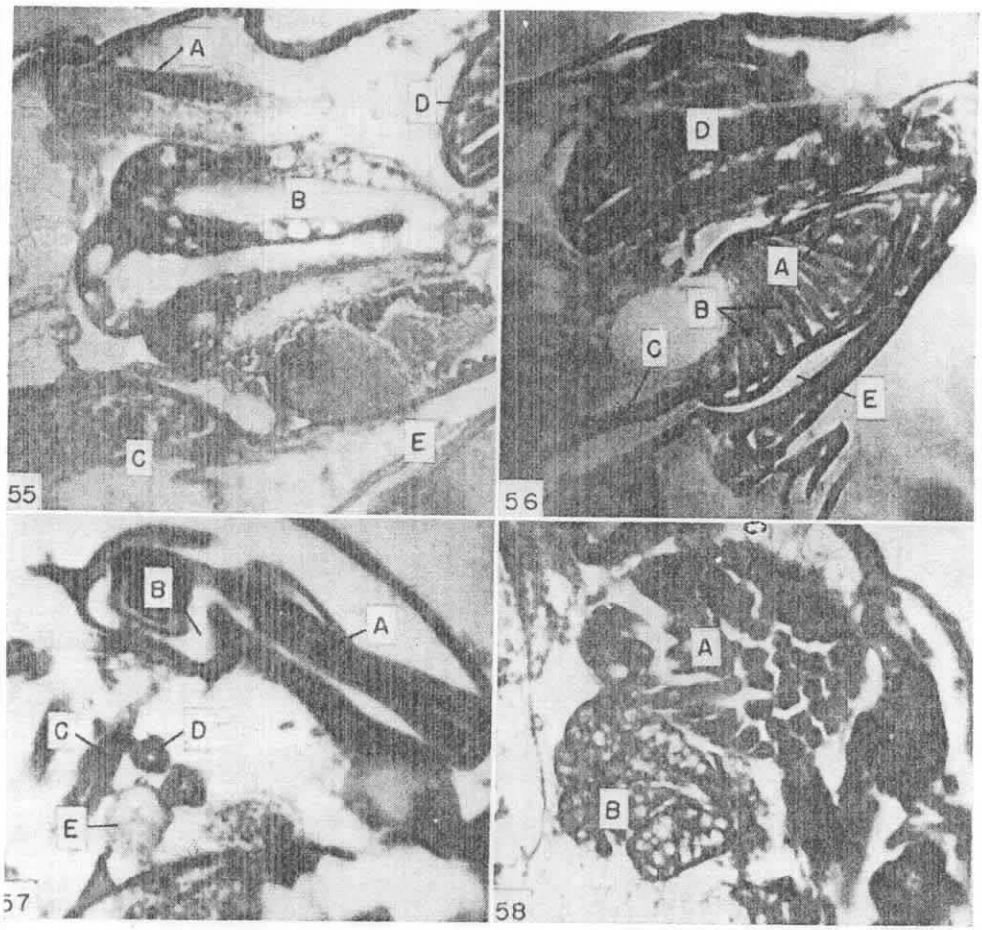


FIG. 55.—Adult: A, cheliceral muscles; B, lumen of salivary gland lobe; C, mesenteron; D, chelicera; E, esophagus. FIG. 56.—Adult gnathosoma: A, orifice of salivary duct; B, pharyngeal muscles; C, esophageal circular muscle; D, chelal muscles; E, pharynx. FIG. 57.—Premolt tritonymph: A, leg bud; B, acetabulum III; C, leg III muscles; D, supracoxal gland; E, coxendral gland. FIG. 58.—Premolt tritonymph: A, podostomatal gland; B, lateral gland.

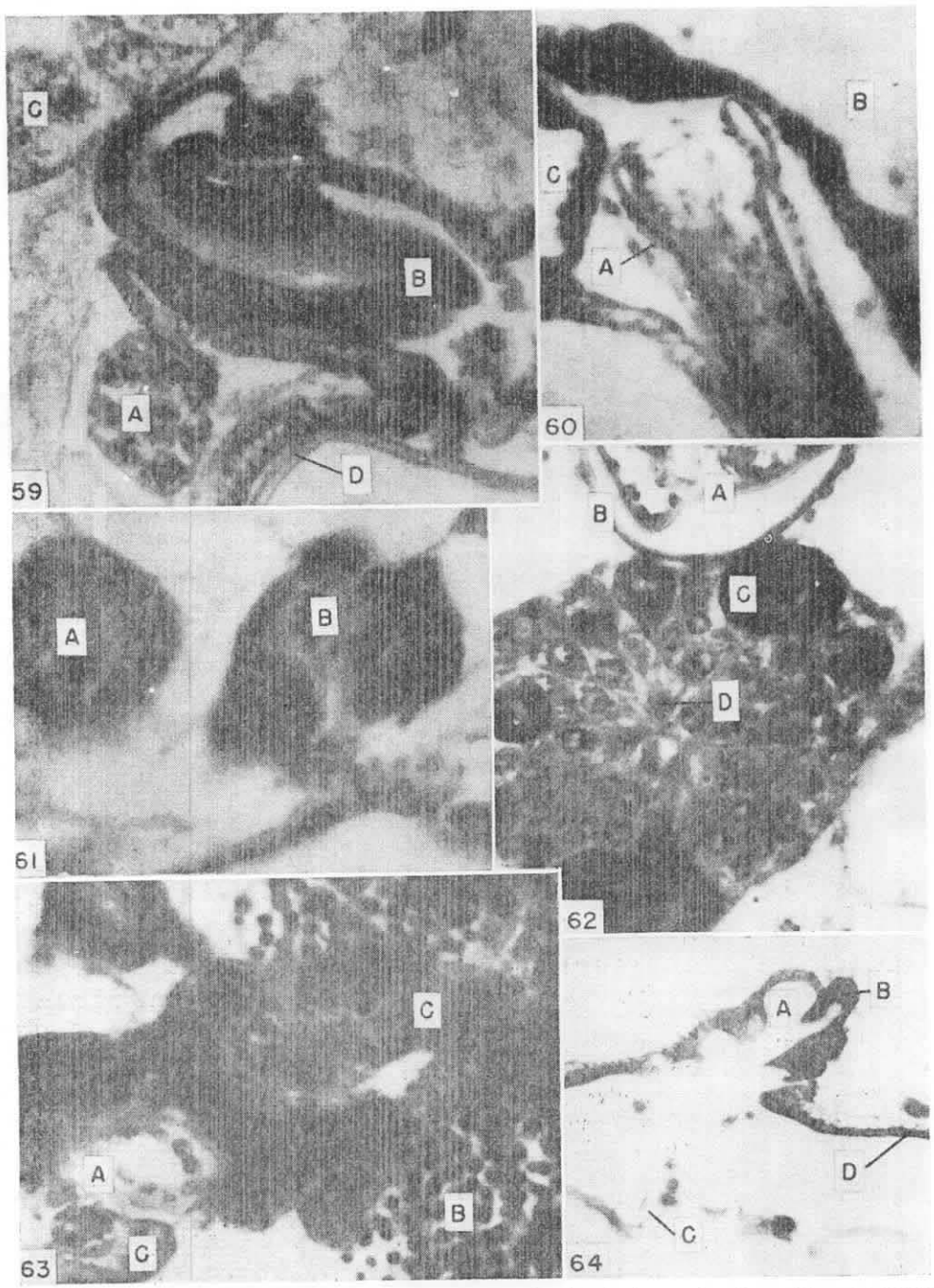


FIG. 59.—Premolt tritonymph: A, young ovary; B, developing ovipositor; C, mesenteron cell; D, tritonymphal cuticle. FIG. 60.—Young adult: A, vagina; B, rectum; C, colon. FIG. 61.—Premolt tritonymph (very young): A, ovary; B, ovipositor bud. FIG. 62.—Young adult: A, distal portion of ovipositor; B, proximal portion; C, mature ovum; D, ovarial stalk (medulla). FIG. 63.—Adult: A, seminal vesicle sphincter; B, testis; C, seminal vesicle cells. FIG. 64.—Premolt tritonymph: A, stalk gland; B, union of vasa deferentia; C, tritonymphal genital disc; D, adult cuticle.